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Aquat. Living Resour. 15 (2002) 335–341

Aquatic Living Resources

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Exotic silver eels *Anguilla anguilla* in Japanese waters: seaward migration and environmental factors

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Received 6 May 2002; accepted 8 October 2002

Abstract

To understand the ecology of the exotic silver European eel *Anguilla anguilla* introduced into Japanese waters, the migratory behavior of 106 specimens captured in the coastal waters of Japan between April 1997 and March 2002 was analyzed. Their migratory behavior was apparently correlated with various environmental factors, particularly photoperiod, water temperature, lunar phase, and passage of atmospheric depressions, and was similar to the behavior of the species in European waters. These findings suggest that transplanted European eels retain their ability to respond to environmental cues for seaward migration in similar temperate habitats. The timing of the migration of silver European eels coincided with that of the native Japanese eels *A. japonica*, suggesting that the silver European eel was synchronized physiologically with the native eel by the same environmental factors. © 2002 Ifremer/CNRS/Inra/IRD/Cemagref/Éditions scientifiques et médicales Elsevier SAS. All rights reserved.

Résumé

***Anguilla anguilla*, l'anguille argentée exotique dans les eaux du Japon : avalaison et facteurs environnementaux.** Afin de comprendre l'écologie de l'anguille européenne argentée, espèce exotique, *Anguilla anguilla*, introduite dans les eaux japonaises, nous avons analysé le comportement migratoire de 106 individus capturés dans la zone côtière du Japon, entre avril 1997 et mars 2002. Leur comportement migratoire est apparemment corrélé aux différents facteurs environnementaux, en particulier, la photopériode, la température de l'eau, la phase de lune et le passage de dépression atmosphérique et il est similaire au comportement de cette espèce dans les eaux européennes. Ces résultats laissent suggérer que les anguilles européennes acclimatées gardent leur capacité à répondre à des stimuli environnementaux, pour la migration vers la mer, en milieu tempéré comparable. La date de la migration des anguilles européennes argentées coïncide avec celle des anguilles japonaises indigènes *A. japonica*, ce qui laisse supposer que l'anguille européenne argentée est synchronisée physiologiquement avec l'anguille japonaise par les mêmes facteurs environnementaux. © 2002 Ifremer/CNRS/Inra/IRD/Cemagref/Éditions scientifiques et médicales Elsevier SAS. Tous droits réservés.

Keywords: Seaward migration; Environmental factor; Exotic species; *Anguilla anguilla*; *Anguilla japonica*

1. Introduction

Silver European eels (*Anguilla anguilla*), after a growth phase in freshwaters where they become adults, migrate from rivers to the sea on stormy nights in autumn (e.g., Deelder, 1954; Winn et al., 1975; Westin and Nyman, 1979; Hividsten, 1985; Pursiainen and Tulonen, 1986; Vøllestad et al., 1986). They then travel thousands of kilometers to their spawning grounds in the Sargasso Sea (Schmidt, 1922; Bertin, 1956; Tesch, 1977).

Onset of the spawning migration of the eels is affected by various intrinsic and extrinsic (environmental) factors. The eels begin to migrate when intrinsic factors such as body size, age and sexual maturity attain a sufficient level (Bertin, 1956; Tesch, 1977; Marchelidon et al., 1999; Durif et al., 2000). Migratory behavior is apparently further controlled by several environmental factors such as decreasing water temperature and lunar periodicity (e.g., Westin and Nyman, 1979; Hividsten, 1985; Pursiainen and Tulonen, 1986;

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PII: S0990-7440(02)01190-7

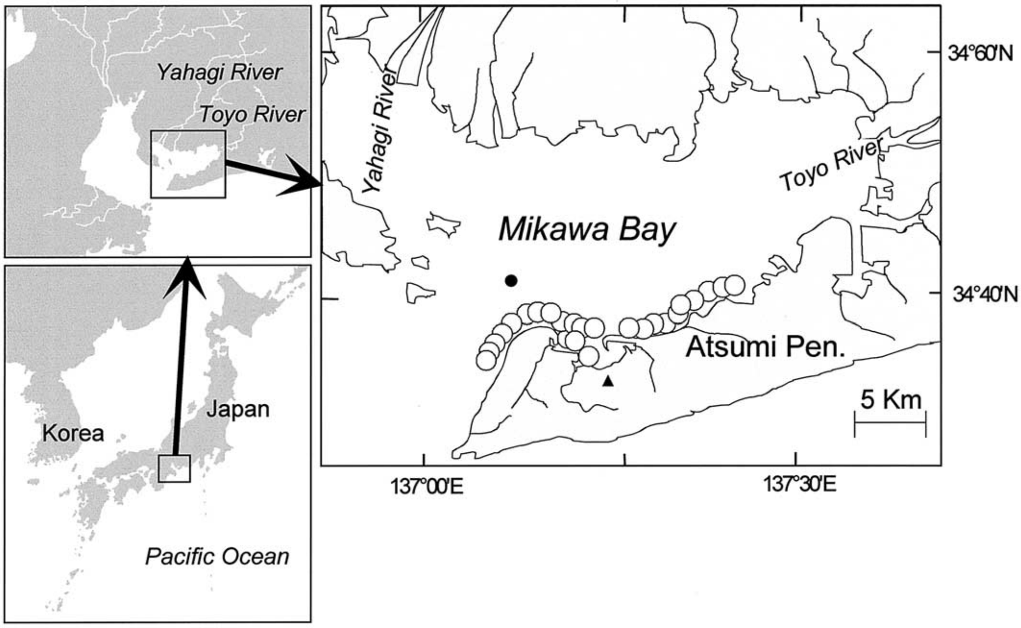

Fig. 1. Map of the study area in Mikawa Bay, Central Japan. Open circles indicate sites of fyke nets for capture of eels. The closed circle indicates an automatic observational buoy. The triangle indicates Irago Weather Station.

Vøllestad et al., 1986; Haro, 1991). Studies on temperate species including New Zealand eels (*A. australis* and *A. dieffenbachii*) suggest that silver eel runs might also be influenced by three other closely related factors: rainfall, increased water level, and the passage of atmospheric depressions (Burnet, 1969; Todd, 1981; Boubée et al., 2001).

Only two eel species, *A. japonica* (Japanese eel) and *A. marmorata* (giant mottled eel), occur naturally in Japanese waters. Probably as a result of escape from aquaculture operations or intentioned release (Tabeta et al., 1977; Zhang et al., 1999), recently the silver European eel has also been found in these waters (Zhang et al., 1999; Aoyama et al., 2000; Okamura et al., 2001). This has led to concern about their impact on native species and has highlighted the need for a better understanding of European eel ecology in local waters, on which little is known.

We collected migrating silver European eels in the coastal waters of Japan and analyzed the relationships between their behavior and environmental variables such as photoperiod, water temperature, lunar phase, and atmospheric depression. This report describes the evidence that these exotic eels behave like native eel species and typically start their migration under the influence of the same environmental factors.

2. Materials and methods

2.1. Sampling

This study was carried out in Mikawa Bay (lat. 34°N, long. 137°E) (Fig. 1), Central Japan, from April 1997 to March 2002. Mikawa Bay has an area of about 200 km^2 with a mean depth of about 12 m. The bay has 20 inflowing streams, including two large rivers (the Toyo and Yahagi), and joins the Pacific Ocean through the Irago Channel.

Eels were caught using 25 fyke nets (Tesch, 1977) placed at depths of 3–10 m, at distances of 50–100 m from the shore, along the coast of the Atsumi Peninsula (Fig. 1). The leader of the nets ranged from about 50–100 m and the larger inner mesh length (mesh size) of the codend funnel was 30 mm. These nets were kept along the coast over the year with sampling undertaken every morning by nine fishermen.

2.2. Species identification

Identification of the species of eels caught was made by the use of two previously described methods (Zhang et al., 1999; Okamura et al., 2001). The specimens caught from April 1997 to March 2000 were genetically identified by PCR–RFLP analysis (Zhang et al., 1999) and the others caught from April 2000 to March 2002, by discriminant function analysis based on external morphological characters (Okamura et al., 2001).

2.3. Environmental variables

Daily photoperiod was calculated by a computer program (MS-Excel, Microsoft). Daily mean seawater temperature, salinity, and dissolved oxygen in Mikawa Bay, recorded by an automatic observational buoy set at a 3.5 m depth (Fig. 1), were obtained from the Aichi Fisheries Research Institute. Daily mean atmospheric pressure and rainfall observed at the Irago Weather Station near the sampling area (Fig. 1) were obtained from the Annual Report of the Japan Meteorological Agency. River water temperature and daily mean water level in the Toyo and Yahagi rivers, observed at about 30 km upstream from their mouth, were obtained from the Yearbook of Japanese Waters (Ministry of Land, Infrastructure, and Transport). Because the patterns of fluctuation in the two rivers were similar, we used the Toyo River data as representative of both rivers in the following analyses.

2.4. Data analyses and statistical treatments

Before analyzing the environmental variables, they were classified into three groups on the basis of their periodicities as follows: (1) seasonal periodic variables—photoperiod, water temperatures, dissolved oxygen and salinity; (2) lunar phase of a 29.5 day periodicity; (3) daily periodic variables—atmospheric pressure, rainfall, water level of the river. Basically, these variables were treated separately in the following analyses.

Although we have attempted to use multiple regression analysis, when testing for possible correlation between the eel catches and environmental variables, we could not obtain a significant partial regression coefficient due to the multicollinearity that was produced by auto-correlated variables (i.e., photoperiod, water temperatures and dissolved oxygen or low pressure, rainfall and river water level). Accordingly, we used simple regression analysis of a linear model in the present analyses.

When testing possible relationships between the catches of European eels and Japanese eels, *t*-tests or χ^2-tests were performed.

3. Results

3.1. Eel characteristics

A total of 2166 freshwater eels were caught. Species identification showed that 106 eels (4.9%) were exotic *A. anguilla* and the remainder (95.1%), native *A. japonica*. The European eels were all females, and had a mean total length (TL) of 79.2 ± 10.1 cm (range: 53.0–104.5 cm, $n = 106$) and mean body weight (BW) 995 ± 405 g (range: 260–2075 g, $n = 106$). It is possible that the sex ratio bias was due to the fyke net size in which only relatively large eels were collected. From dissection, the mean gonadosomatic index (GSI = gonad weight $BW^{-1} \times 100$) of 1.7 ± 0.9 (range: 0.6–4.8, $n = 24$) and the mean eye index (eye area$\cdot TL^{-1} \times 100$) (Pankhurst, 1982) of 10.7 ± 1.9 (range: 6.6–14.9, $n = 51$) indicated that most of the specimens were sexually maturing or had reached the migratory silver phase (Pankhurst, 1982).

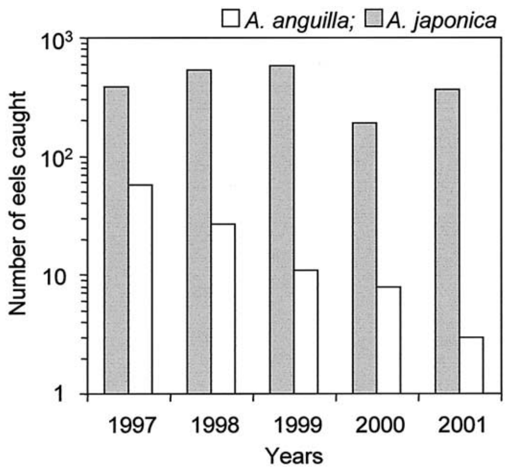

Fig. 2. Yearly (1 April of year noted through 31 March of following year) catch of European eels *Anguilla anguilla* (open bars) and Japanese eels *A. japonica* (shaded bars) in Mikawa Bay, from April 1997 to March 2002.

3.2. Catch history

Of the total 106 silver European eels collected, 57 were caught in the first year (April 1997–March 1998), 27 in the second (April 1998–March 1999), 11 in the third (April 1999–March 2000), eight in the fourth (April 2000–March 2001), and three in the last (April 2001–March 2002) (Fig. 2), indicating that the European eel population appeared to annually decline while the yearly catch of Japanese eels was roughly constant during the study. Although the yearly catch changes in both species were significantly independent of each other (χ^2-test, $P < 0.01$), at present, we have not identified a physical factor to explain the decreasing European eel catches.

As with Japanese eels (Okamura et al., 2002), the catch of European eels also fluctuated seasonally (Fig. 3) with few being caught from spring to late summer (April–September), and the majority being caught during autumn and winter (October–January). The timing of seasonal (monthly) catch in both species statistically coincided with each other during the 1997–1999 seasons (χ^2-test, $P > 0.2$).

3.3. Photoperiod, water temperature, dissolved oxygen and salinity

Eel catches seemed to be associated with decreasing day length and water temperatures (Fig. 3). To test the relationship between the monthly catches and monthly photoperiod or water temperatures, simple regression analyses were done (Table 1). The monthly data of dissolved oxygen and salinity were also analyzed (Table 1). From these results, it was determined that there were significant negative correlations between the monthly catches and photoperiod or river water temperature, but there was no correlation between the eel catches and seawater temperature, dissolved oxygen or salinity in Mikawa Bay (Table 1).

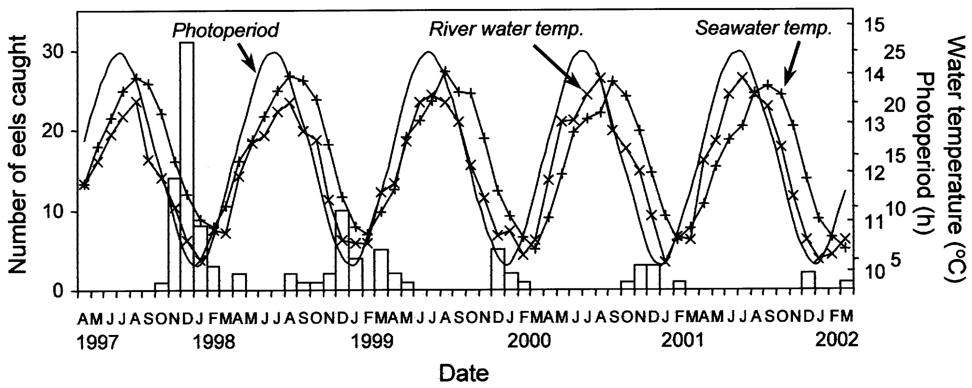

Fig. 3. Relationship of monthly catch of European eels *Anguilla anguilla* in Mikawa Bay and photoperiod and monthly mean temperature of the Toyo River, Central Japan, from April 1997 to March 2002.

Maximum catches of both species occurred when the seawater temperature was 13 to 15 °C and the river water temperature was 8 to 10 °C, and the timing of occurrence of both mostly overlapped (Fig. 4). However, the mean water temperature of all European eel catches (Mikawa Bay, 13.0 °C; Toyo River, 8.3 °C) was significantly lower than that of Japanese eels (Mikawa Bay, 14.6 °C; Toyo River, 10.1 °C) (t-test, $P < 0.05$), and both frequency distributions (Fig. 4) were statistically independent from each other (χ^2-test, $P < 0.001$). Similar results were also obtained when analyzing the correlation with photoperiod.

3.4. Lunar phase

Eel catches were significantly synchronized with the lunar phase as follows: maximum catches coincided with the new moon and remained relatively large during the first quarter, but were relatively small during the full moon and last quarter, even when the moon was completely shaded by clouds (Fig. 5; Table 2).

3.5. Atmospheric depression, rain, and river water level

In the Mikawa area, rainfall during autumn and winter (October–January) is less than in other seasons. Although atmospheric depressions pass through Mikawa Bay during this season, they produce only gusty winds or a little rain. From October to January 1997–2002, there were at least 290 depressions—a depression is defined in this paper as a day on which the atmospheric pressure was lower than on the previous day—in the bay area. However, rainfall (>0.5 mm day^{-1}) accompanied about 50% of these depression days, and an increasing river water level (>0.01 m day^{-1}) was associated with about 40% of the depression days.

Based on a report from a local fisherman that eels were frequently caught several days after an atmospheric depression, with or without rainfall, we plotted the number of occasions (eel-days) on which European eels were caught in the days following the occurrence of one of the three factors: depressions, rainfall, and an increasing river water level (Fig. 6). This clearly showed that most eel-days (47%) occurred 2 days after the passage of a depression rather than after both rainfall and increased river water level (Fig. 6).

Simple regression analysis between the three daily independent variables (atmospheric pressure, rainfall and river water level) and the daily eel catches showed that each variable was correlated significantly with the daily catch data on the two days after each occasion of the three factors (Table 3), and did not show any significant correlation with the daily catch data on other days.

4. Discussion

Studies on spawning migration of eels in the temperate zone including Europe, America and New Zealand have shown that their migratory behavior is probably controlled

Table 1
Simple regression analyses between the monthly catch of silver European eels *A. anguilla* (Y_M) and the monthly data of four environmental variables (X), from April 1997 to March 2002

Independent variables	Regression equations	R^2	F	P
Photoperiod (d; X_P)	$Y_M = -28.25X_P + 16.34$	0.16	11.07	0.001
River water temperature [a] (°C; X_{RT})	$Y_M = -0.22X_{RT} + 4.97$	0.11	7.50	0.008
Sea water temperature [b] (°C; X_{ST})	$Y_M = -0.15X_{ST} + 4.19$	0.05	2.84	0.10
Dissolved oxygen [b] (%; X_{DO})	$Y_M = 0.04X_{DO} - 1.46$	0.04	2.56	0.11
Salinity [b] (‰; X_S)	$Y_M = 0.007X_S + 1.54$	<0.001	<0.001	0.99

[a] Data in the Toyo River.
[b] Data in Mikawa Bay.

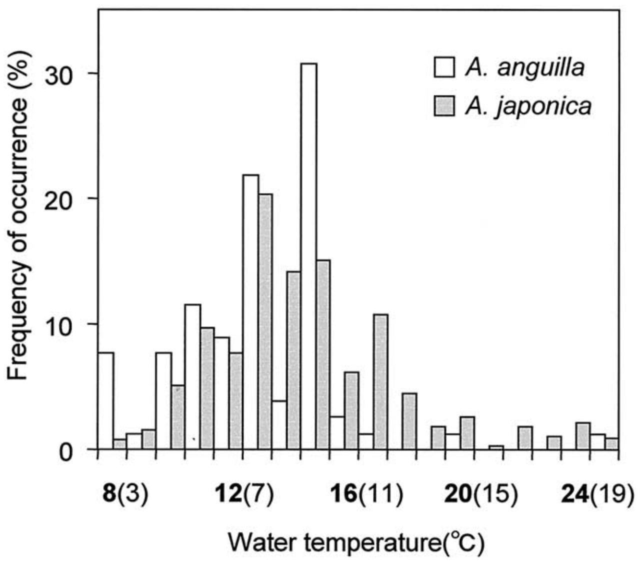

Fig. 4. Relationship of frequency of catches of European eels *Anguilla anguilla* (open bars) and Japanese eels *A. japonica* (shaded bars) in Mikawa Bay along Atsumi Peninsula coast to water temperatures from April 1997 to March 2002. Temperatures in boldface indicate that in Mikawa Bay, and in parentheses in the Toyo River at the same time.

by several environmental factors including water temperature, lunar phase, atmospheric depressions, and increasing river water levels. We have demonstrated that these same factors influence silver European eel migration in Japanese waters. These facts suggest that European eels have developed normally in Japanese aquatic ecosystems, retaining their ability to react to particular signals from the environment. This might be due to the similarities of the environment in the study area to those in Europe.

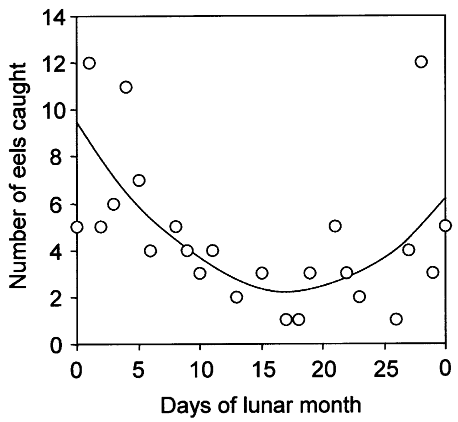

Fig. 5. Number of European eels *Anguilla anguilla* caught each day in a lunar month in Mikawa Bay, Central Japan, from April 1997 to March 2000.

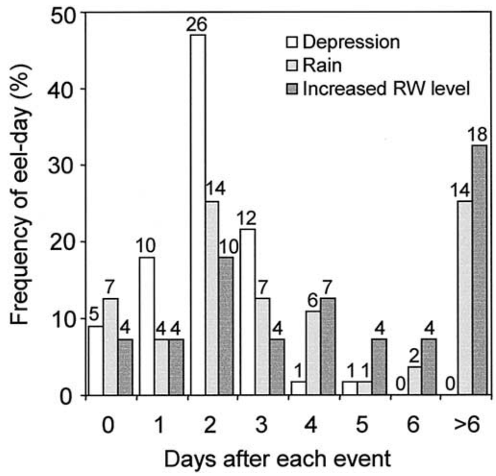

Fig. 6. Frequency of eel-days (days on which European eels *Anguilla anguilla* were caught) in the days following the passage of a depression, rain, and increased river water (RW) level in the Mikawa Bay area, Central Japan, from April 1997 to March 2002. Numerals on the bars represent the number of eel-days.

4.1. Photoperiod and water temperature

The influence of a decreasing photoperiod and river water temperature on eel migration could not be determined separately because of their strong correlation ($r = 0.91$, $P < 0.0001$), however, the influence of the latter on eel migration has been well documented (e.g. Westin and Nyman, 1979; Vøllestad et al., 1986; Hividsten, 1985; Pursiainen and Tulonen, 1986; Haro, 1991). That of the photoperiod has not yet been well documented, although Zaugg (1981) has shown that it is an important factor affecting the migration of the steelhead *Salmo gairdneri*. Vøllestad et al. (1986) attempted to compare these two related factors but did not succeed. The present study again showed that the two factors equally correlated with eel catches, but could not determine which factor was more significant.

Our analyses showed that the seawater temperature, dissolved oxygen or salinity did not relate to eel migration (Table 1), although all eels were caught in Mikawa Bay. However, the river water temperature and photoperiod significantly correlated with eel migration (Table 1). This result suggests that pre-migratory eels usually stayed in the rivers, sensed the alteration of photoperiod or river water temperature there, and then began their migration toward the sea. Our catch data in the bay thus represents the result of activity of silver eels in the rivers.

The optimal river water temperature when silver European eels migrated down into Mikawa Bay (8 to 10 °C; Fig. 4) coincides well with that in Europe (Vøllestad et al.,

Table 2
Simple regression analysis between the daily catches of European eels *A. anguilla* (Y_D) and the days of lunar month (X_L) as independent variables, from April 1997 to March 2002

Independent variable	Regression equation	R^2	F	*P*
Photoperiod (*d*; X_L)	$Y_D = -0.77X_L + 0.02X_L + 9.02$	0.38	6.01	0.009

Table 3
Simple regression analyses between the daily catches of European eels *A. anguilla* (Y_D) and the three daily environmental data (X) on the 2 days before the catch, from April 1997 to March 2002

Independent variables	Regression equations	R^2	F	P
Atmospheric pressure [a] (hpa; X_{AP})	$Y_D = -0.13X_{AP} + 2.03$	0.14	8.21	0.006
Rainfall [b] (mm; X_R)	$Y_D = 0.10X_R + 1.54$	0.50	52.02	<0.001
River water level [c] (m; X_{WL})	$Y_D = 2.63X_{WL} + 1.93$	0.15	9.62	0.003

[a] Daily difference from previous day. Lower limit detection: 0.1 hpa.
[b] Daily total rainfall. Lower limit detection: 0.5 mm.
[c] Daily difference from previous day. Lower limit detection: 0.01 m.

1986), suggesting that European eels in Japan have well retained the sensitivity to such environmental signals. However, the water temperature at which European eels migrated was lower than of Japanese eels (Fig. 4), suggesting that silver European eels have a different sensitivity to this environmental signal than silver Japanese eels. Similar interpretations are also given when analyzing the optimal photoperiod for the peak catches.

4.2. Lunar phase

The migratory activity of silver European eels in Japanese waters was influenced by the lunar phase, with peak movements occurring mainly around the new moon (Fig. 5). This result is well consistent with that of Japanese eels occurring in Mikawa Bay (Okamura et al., 2002), but quite dissimilar to its activity in European, American and New Zealand waters where it usually migrates during the last quarter of the lunar month (Deelder, 1954; Winn et al., 1975; Hividsten, 1985; Pursiainen and Tulonen, 1986; Todd, 1981). This difference may be explained by the difference in study sites in that previous studies were done in rivers (Deelder, 1954; Winn et al., 1975; Hividsten, 1985; Pursiainen and Tulonen, 1986; Todd, 1981), while ours was done in a bay. This difference could have caused the time-lag, and if so, the peak movements occurring around the new moon could be calibrated as having been the result of higher activity of silver eels in the rivers around the last quarter.

The higher migratory activity influenced by the lunar phase is thought to be regulated by an innate activity following a circa-lunar rhythm (Deelder, 1954; Boëtius, 1967; Todd, 1981; Jens, 1952–1953; Tesch, 1977). However, some possibility should be mentioned in our case that the peak catches occurring around the new moon in the bay might be influenced by effectiveness of nets varied with lunar phase, i.e. strength or direction of tides relative to neap and sprig stages.

4.3. Atmospheric depressions

The peak catches of silver European eels frequently occurred 2 days after the passage of depressions (Fig. 6), suggesting that their migratory behavior might be affected by these depressions. This result is well in accord with that of silver Japanese eels occurring in Mikawa Bay (Okamura et al., 2002). have suggested that silver Japanese eels migrating down from the upstream of rivers do not enter the sea immediately, but stay at river mouth for various physiological acclimation to seawater for several days, then they start to enter the sea when a depression arrives. If so, about 2-day lag between depression days and the capture of silver eels by the nets (Fig. 6) may be accounted for by the distance from the river mouth to the locations of the nets.

In previous studies, depressions might have been usually accompanied by rain and increasing river water levels, but was difficult to determine which factor was the most important (Burnet, 1969; Todd, 1981; Vøllestad et al., 1986; Boubée et al., 2001). Our regression analyses also showed that each variable equally correlated with the daily eel catches in similar significance (Table 3). However, these environmental factors did not always occur simultaneously (Fig. 6), enabling us to determine that the migratory activity of silver European eels in Japan was affected more by the passage of a depression than by rain or increased river water level. This finding may likely also be the case in Europe or other areas.

4.4. Possible impact on native ecosystems

Silver Japanese eels also occur in Mikawa Bay during autumn and winter (Okamura et al., 2002). The migratory behavior of these eels is also affected by water temperature (or photoperiod), the lunar phase, and depressions, which mostly coincides with that of the European eels (Okamura et al., 2002). Thus, the migration of silver European eels may have become synchronized physiologically with Japanese silver eels following the same environmental cues. Zhang et al. (1999) suggested that European eels would not migrate with Japanese eels to the spawning area of the latter in the Pacific Ocean and, therefore, could not genetically contaminate the populations of Japanese eels. However, our findings may not support this suggestion. We feel that it is possible for them to migrate together toward the open ocean, although whether the European eels reach the Japanese eels' spawning ground is unknown. Aoyama et al. (2000) reported that a mature European eel was caught in the East China Sea at least 70 km from the nearest freshwater habitat, which also suggests the possibility of genetic contamination.

The catches of silver European eels decreased gradually in Mikawa Bay during the study (Fig. 2). This decline may be attributed to the decrease recruitment as a result of the recent reduction of European eel culture in Japan (Oka and Egusa, 2001). However, European glass eels are still freely imported into East Asia, including China and Korea for aquaculture (Dekker, 2001), and the potential for the dispersion of European eels into East Asian waters yet exists. Thus, further studies of their distribution and ecology within other waters of East Asia are needed to assess impact on native aquatic ecosystems.

Acknowledgements

We thank nine fishermen and members of the IRAGO Institute for their kind cooperation in collecting and dissecting samples. We also thank Dr. Jun Aoyama for providing valuable literature. This work is a contribution (No. 018) of the IRAGO Institute.

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